COMPOSITION OF THE SWIMBLADDER GAS IN DEEP SEA FISHES [1]

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In an earlier study of the composition of the swimbladder gas in bottom-dwelling marine fishes caught at depths down to 220 meters, it was found that at all depths the partial pressure of nitrogen in the swimbladder was usually close to that of the surrounding sea water, *i.e.*, 0.8 of an atmosphere (Scholander, Claff, Teng and Walters, 1951). CO_2 was present only in traces, and thus the pressure build-up above 0.8 atmosphere seemed to be due to oxygen only. A slight but definite increase in the nitrogen pressure with depth was apparent from the data, but this was considered at least partly to be an artifact due to changes in the gas composition after the catch.

Non-bottom-dwelling species were often found to have a partial pressure of nitrogen in their bladders far above 0.8 of an atmosphere. These fishes were in buoyancy equilibrium at a very shallow depth, and hence might have acquired their high nitrogen values when equilibrating at much lesser depths than that at which they were caught, *i.e.*, as a consequence of vertical migrations.

In the summer of 1952 we had the opportunity to extend the survey down to a depth of some 950 meters, *i.e.*, about four to five times deeper than before, with the result that now a fuller and more accurate picture of the performance of the gas gland in relation to depth can be presented.

Material

Material for the present investigation was obtained at the Lerner Marine Laboratory, Bimini, Bahamas, December 24, 1951, to January 2, 1952, and during two trawling cruises from the Woods Hole Oceanographic Institution. The latter were conducted off the New England coast by the dragger *Cap'n Bill II* from July 10 to 17 and 23 to 30, 1952. Some 260 specimens were analyzed, covering 29 species of fish caught between 120 and 950 meters' depth.

At the Lerner Marine Laboratory the fishes were obtained at depths of 300–420 meters. They were caught at the bottom on a baited hook fastened to a heavily weighted wire line and were pulled to the surface within 3–5 minutes by means of a motor driven reel. The wire passed over a meter wheel which indicated the depth. Gas samples from the following species were analyzed:

Epinephelus	Grouper
Epinephelus mystacinus	Black grouper
Lutianus vivanus	Long-fin red snapper

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Fishing on the *Cap'n Bill* was done by means of an otter trawl, dragging the bottom for 30 minutes. The time of ascent of the net from the bottom to the surface may be estimated at about 30 minutes for the greatest depths. The depth of the stations was continuously indicated on a fathometer. Gas samples from the following fishes were taken and analyzed on board:

		Known depth range in meters
Alepocephalus sp.		890
Antimora viola	Blue hake	560–1830
Argentina silus	Herring smelt	60–670
Coryphaenoides rupestris	Round-nose ratfish	700–2200
Cottunculus thomsonii	Deep sea sculpin	190–1570
Dicrolene sp.		840–890
Macrourus bairdii	Common ratfish	140–2300
Macrourus berglax	Smooth-spined ratfish	180–1240
Merluccius bilinearis	Silver hake	0–870
Notacanthus phasganorus		870
Peristedion miniatum	Deep sea robin	170–350
Sebastes marinus	Rosefish	30–1680
Simenchelys parasiticus	Slime eel	360–1620
Synaphobranchus pinnatus	Long-nosed eel	240–2660
Tautogolabrus adspersus	Cunner	0–130
Urophycis chesteri	Long-finned hake	60–990
Urophycis chuss	Squirrel hake (ling)	0–540
Urophycis regius	Spotted hake	160
Urophycis tenuis	White hake (ling)	0–540

The data on the depth range are taken from Bigelow and Welsh (1924) and from Goode and Bean (1895), or are from our own records.

Methods and Reliability of Data

The micro-gas-analytical method used gives the carbon dioxide and oxygen percentages through absorption with KOH and alkaline pyrogallol[2] respectively (Scholander *et al.*, 1951). The accuracy is about ± 0.2 to ± 0.3 per cent of the true value. The unabsorbed fraction ("nitrogen") of the gas sample, in addition to nitrogen, may contain noble gases and organic gases.

The amount of organic gases was determined by combustion in a separate chamber and subsequent analysis for CO_2 in the one-half cc. analyzer (Scholander, 1947). The plungers of the syringes with which the samples for these analyses were taken had been lubricated with concentrated lithium chloride solution, and care was taken throughout to avoid organic contaminations. The results are given in Table I and show that the amount of CO_2 formed by combustion of the swimbladder gas is usually no more than a few hundredths of one per cent. Hence organic gases play no significant role in the build-up of the gas pressure in the swimbladder of deep sea marine fishes. The traces of organic gases present in the samples may have been derived from bacterial activity in the gut of the fish.

[2] In the described technique the oxygen is absorbed by running a large excess of fresh pyrogallol down over the gas bubble. This procedure keeps carbon monoxide formation down to sub-detectable values, even in samples of pure oxygen, and agrees with results obtained by Kilday (1950), who used essentially the same absorption principles in a Haldane-type macro-method.

No carbon monoxide could be detected in gas samples from *Urophycis chesteri* and *Macrourus berglax*. Other species were not tested.

Schloesing and Richard (1896) analyzed the swimbladder gas of *Muraena helena* caught at 88 meters' depth and found that the argon over nitrogen-plus-argon ratio was 1.85%. Similarly in *Synaphobranchus pinnatus,* caught at 1385 meters' depth, the ratio was 1.94%. With a ratio in air of 1.18%, this means about a 60% increase in the argon over nitrogen-plus-argon ratio in these fishes. The samples were small and the analyses were not considered very accurate, although probably significant as to the increase mentioned. We have as yet no data on the content of argon in our material.

In our discussion of the correlation of the gas composition with depth we have assumed (a) that the fish are in a steady state of equilibrium at the depth of the catch, *i.e.,* that they have remained at this depth for a substantial period of time, and (b) that this gas composition has not changed materially since the time the fish was caught.

TABLE I

Carbon dioxide content of swimbladder gas before and after combustion

Species	Depth of catch (m.)	% N_2	% CO_2		ΔCO_2
			Before Combustion (a)	After Combustion (b)	(b)-(a)
Antimora viola	820	7.8	1.31	1.32	0.01
	820	7.2	0.84	0.90	0.06
Coryphaenoides rupestris	720	10.0	0.18	0.19	0.01
	720	11.6	0.67	0.72	0.05
	720	—	0.85	0.96	0.11
Macrourus bairdii	820	8.2	0.03	0.16	0.13
	610	8.2	0.65	0.67	0.02
Sebastes marinus	440	11.2	0.37	0.38	0.01
	440	—	0.34	0.41	0.07
Synaphobranchus pinnatus	820	6.2	1.96	1.98	0.02
Urophycis tenuis	610	7.8	0.37	0.40	0.03
	610	5.8	0.20	0.20	0.00
	610	6.2	0.18	0.19	0.01

As to the first assumption, we know that the Bimini fishes were at the bottom when they were caught, and Bigelow and Welsh (1924) consider most of our northern deep sea species as decidedly bottom-dwelling species. To what extent these fishes might migrate up and down along the bottom slope is not known.

As to the second assumption, there is good evidence that the changes in gas composition that take place from the time the fish is caught until the time the gas

sample is secured are so small that they could not change the conclusions significantly. Thus, the Bimini fishes, which were secured between five and ten times faster than the northern fishes, gave results which superimposed on the northern data. Two sets of experiments showed that changes in the gas composition after the catch occur only slowly. Bloated and more or less moribund individuals of eight species of our deep sea fishes, left on deck, in or out of water, showed an increase of at most one per cent in the nitrogen percentage in 30 minutes. In two species of fishes from much shallower depths, as reported earlier, the increase was larger, but still insignificant when compared with the total nitrogen.

In other experiments oxygen was injected into the peritoneal cavity of two remoras (*Echeneis naucrates*) and one puffer (*Spheroides maculatus*), caught in shallow water. The amount injected was about ten times the amount of swimbladder gas normally present in fishes of similar weights. In these fully alive fish the nitrogen per cent of the injected gas increased in half an hour by 1.4 and 0.4%, respectively. A fish at 1000 meters' depth contains 100 times as much gas as a surface fish, and if such an amount could have been injected into these remoras or the puffer the percentage nitrogen increase would have been entirely negligible.

Also, simple calculation shows that even if the entire amount of nitrogen dissolved in the tissues of a fish were transferred into the swimbladder, which was then expanded 100 times, the increase in the nitrogen would amount to only a few tenths of a per cent. Finally, the amount of oxygen present in a swimbladder at 100 atmospheres' depth is so great that respiratory oxygen removal could not materially change the nitrogen percentage either. We feel, therefore, that our data must reflect essentially the conditions which existed in the swimbladder when the fish was caught.

Composition of the Swimbladder Gas in Relation to Depth

In Figure 1 a composite diagram is presented of the previous (Scholander *et al.*, 1951) and present data, extending from the surface forms to the deep sea forms at 950 meters. The diagonal straight line represents a nitrogen percentage which corresponds to a partial pressure of nitrogen of 0.8 atmosphere, *i.e.*, that of the surrounding sea water. We assume here that nitrogen values to the right of this line are due to something other than diffusion equilibrium and that the balance of the pressure is due to oxygen secretion. It is clear from the figure that the nitrogen values found at greater depths deviate increasingly from the line showing the atmospheric nitrogen tension.

Figure 2 shows the partial pressures of the nitrogen and oxygen as calculated from the percentages found and from the depths at which the fish were taken. In fishes living near the surface the nitrogen and oxygen tensions were generally found to be close to those in air, indicating that here the diffusion exchange between the swimbladder and the outside water dominates the picture. From the surface value of 0.8 atmosphere the nitrogen pressure increases in an over-all linear fashion with depth, often attaining values as much as 10 to 15 atmospheres higher than the nitrogen tension in the surrounding sea water.

Much of the considerable spread in the data in Figure 2 is due to specific differences among the fishes. In Figure 3 we have plotted the nitrogen for four species of fish, covering a wide range of depth. It is indicated that the increase in

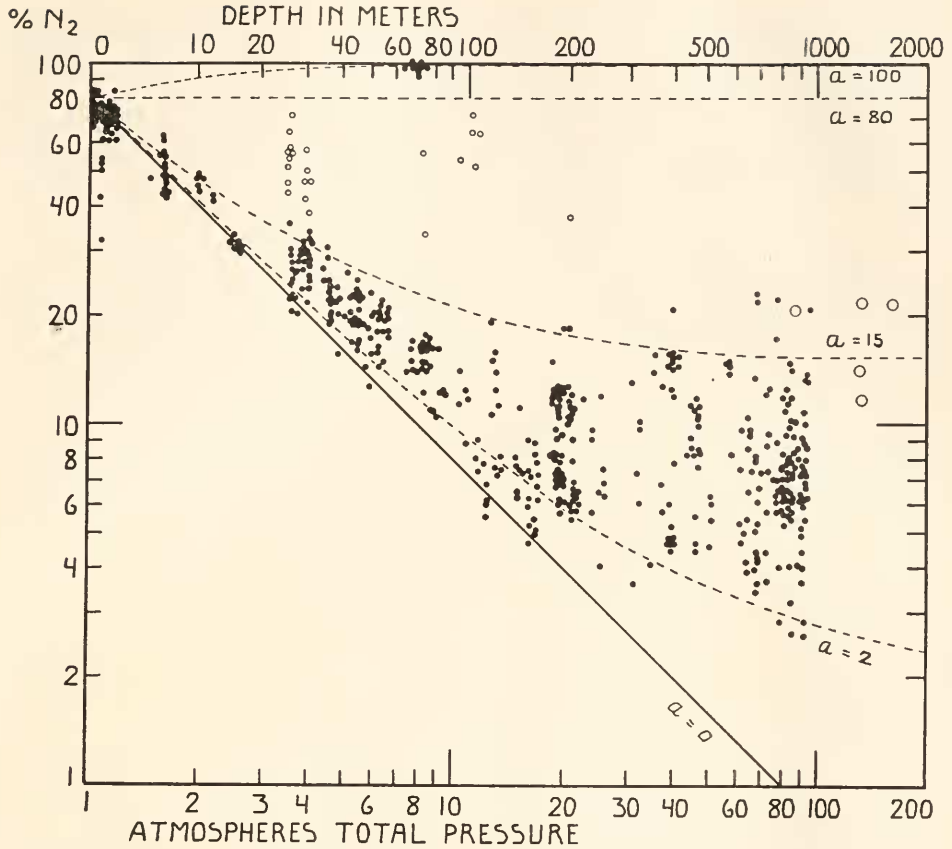

FIGURE 1. Composite graph of the nitrogen concentration found in swimbladder gas from fishes at various depths. The diagonal full-drawn line represents the percentage of nitrogen which at any given depth would give a partial pressure of nitrogen of 0.8 atmosphere. Both the present and previous data (Scholander *et al.*, 1951), as well as Hüfner's data (1892) for *Coregonus* (near 100% N_2), are given by solid circles. The large open circles are data on *Simenchelys parasiticus* (1674 m.) and *Synaphobranchus pinnatus,* given by Schloesing and Richard (1896). The small open circles are data from scup and silver hake, where the high nitrogen most likely is due to vertical migration. The dotted lines represent percentages of the total gas pressure due to nitrogen corresponding to values for *a* of equation (1). The empirical data indicate that *a* in our material lies usually between 2 and 15.

nitrogen tension with depth in each species is more or less linear, the curves for the different species having individual slopes. These differences are also apparent in Figures 4 and 5.

Sebastes is a fish that apparently stays at the bottom in the daytime, but moves off the bottom at night. This could tend to produce a nitrogen value higher than that corresponding to the bottom depth (Scholander *et al.*, 1951). However, high nitrogen is also found in species like the deep sea sculpin, *Cottunculus,* and many others which are most likely always in close proximity to or on the bottom. Many

of these fishes caught at depths of 900–1000 meters have a nitrogen percentage so high that they would have to move up to 100 meters' depth, or shallower, if their nitrogen were to be explained by simple diffusion from the sea water. Such vertical migrations are clearly out of the question for most of our fishes, and we are therefore forced to assume that nitrogen as well as oxygen can be deposited in the swimbladder against very considerable pressure gradients. This, of course, corroborates Hüfner's findings (1892) of nitrogen secretion in the whitefish.

Relation Between Gas Deposition by Diffusion and Secretion

The swimbladder gas may be resolved into two main components. One is derived from diffusion exchange with the outside sea water. The other constitutes

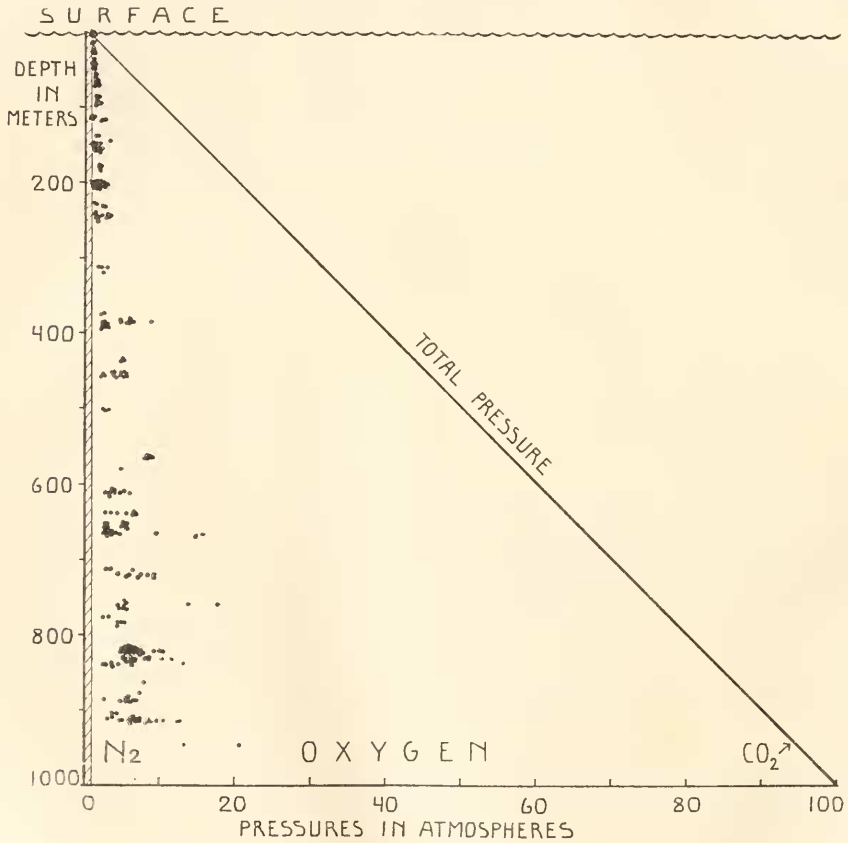

Figure 2. The partial pressures of nitrogen, oxygen and CO_2 calculated from the percentages and the depths. The shaded area is equal to the partial pressure of nitrogen in the sea water. The partial pressure of nitrogen in the swimbladder is to the left of each point, of oxygen to the right. The partial pressure of the CO_2 is usually less than what is represented by the thickness of the drawn diagonal line. The over-all picture suggests a linear increase in the partial pressure of the nitrogen with depth.

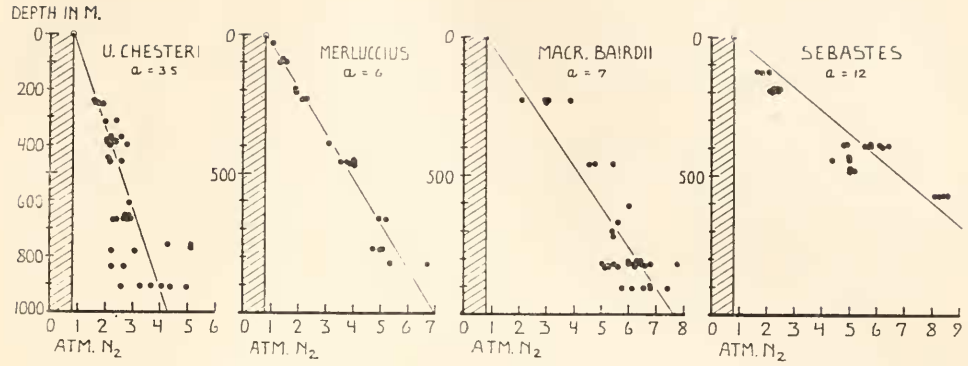

FIGURE 3. Partial pressures of nitrogen in the swimbladders of *Urophycis chesteri, Merluccius bilinearis, Macrourus bairdii,* and *Sebastes marinus.* The data suggest that the nitrogen in excess of 0.8 atmosphere increases linearly with depth from a value of zero at the surface. The different slopes of the lines indicate that the proportions of nitrogen and oxygen secreted are different in different species.

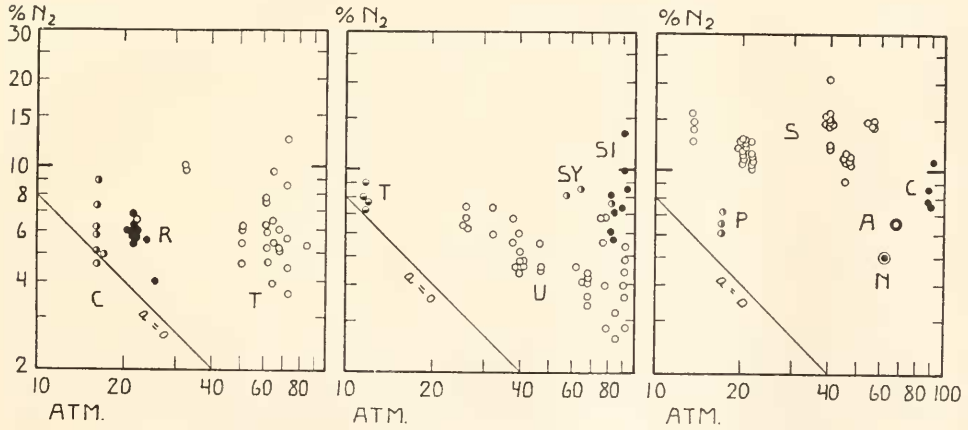

FIGURE 4. Gas composition in the swimbladder in relation to total pressure. Left: *Urophycis chuss* (C), *Urophycis regius* (R), *Urophycis tenuis* (T). Middle: *Tautogolabrus adspersus* (T), *Urophycis chesteri* (U), *Simenchelys parasiticus* (SI), *Synaphobranchus pinnatus* (SY). Right: *Peristedion miniatum* (P), *Sebastes marinus* (S), *Cottunculus thompsonii* (C), *Notacanthus phasganorus* (N), *Argentina silus* (A). These fishes were taken off the New England coast. The N_2 percentages of *Simenchelys* and *Synaphobranchus* obtained by Schloesing and Richard (1896) are entered on Figure 1. They are about twice as great as those shown from our data on these species.

what may be called the secreted [3] part which is responsible for the pressure build-up. As the nitrogen tension is known to be constant and very near to 0.8 atmosphere at all depths (Rakestraw and Emmel, 1938; Hamm and Thompson, 1941), we shall

[3] We shall use the word "secretion" to mean any process whereby gases are deposited into the swimbladder so as to increase potentially or really the partial pressure above that in the ambient medium.

discuss below mainly the nitrogen deposition in the swimbladder. The same considerations may be applied also to the oxygen deposition, although here the picture may be somewhat blurred by the fact that the oxygen tension in the sea water varies considerably.

If a fish remains for a long time at a definite hydrostatic pressure where it maintains a neutral buoyancy, one may assume that the gas entering the swimbladder will be equal to that leaving the swimbladder in amount as well as in composition. Where such a steady-state situation obtains, the quantitative relation of the gas composition to the depth may be empirically described as the resultant of (1) a diffusion exchange term and (2) a gas secretion term.

The diffusion exchange component would lead to a partial pressure of nitrogen equal to the partial pressure in sea water, 0.8 atmosphere, times a factor, F, expressing the completeness of equilibrium between the swimbladder gas and the sea water, *i.e.*, $0.8 \times F$.

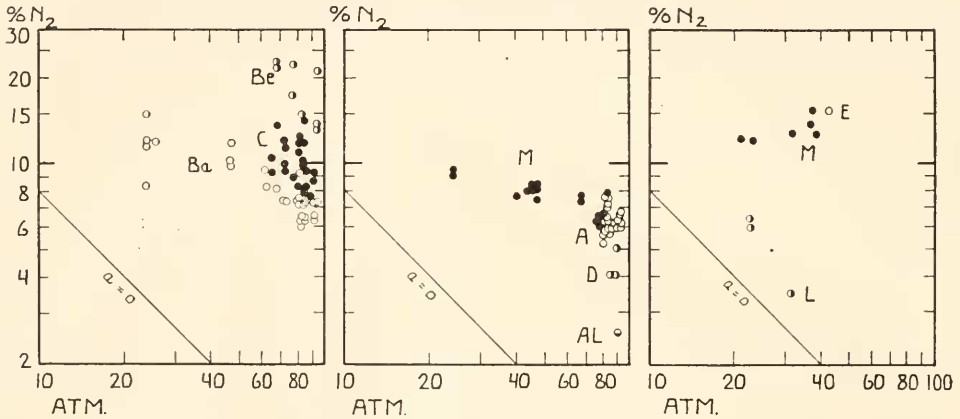

FIGURE 5. Gas composition in the swimbladder in relation to total pressure. Left: *Macrourus bairdii* (BA), *Macrourus berglax* (BE), *Coryphaenoides rupestris* (C). Middle: *Merluccius bilinearis* (M), *Antimora viola* (A), *Dicrolene* sp. (D), *Alepocephalus* (AL). Right: *Epinephelus mystacinus* (M), *Lutianus vivanus* (L), *Epinephelus* (E). The last three fishes were taken off Bimini. All the others were caught off the New England coast.

The gas secretion component represents an additional quantity of nitrogen which has entered the swimbladder as the result of secretion and which increases the partial pressure by an amount represented by $\frac{a}{100} \times D$, where a is the percentage of nitrogen present in the swimbladder as the result of secretion and D is the depth in atmospheres.

The total partial pressure, P_{N_2}, is thus given by

$$P_{N_2} = (0.8 \times F) + \left(\frac{a}{100} \times D\right) \tag{1}$$

The factor F is introduced into the diffusion term for the following reason. Near the surface D is small and in most fishes the gas diffusion exchange with the

sea water is so complete that a near-air composition is maintained in the swimbladder. This does not hold for all species, however. Even when kept in a shallow tank for a long time tautogs usually have much less than 80% N_2 in their swimbladders (Safford, 1940; Scholander *et al.*, 1951, Fig. 7). This fish, then, seems to have an exceptionally well developed isolation of its swimbladder with respect to diffusion, and this may be expressed by a factor F which is smaller than one. Although difficult to verify, it seems likely that deep sea fishes would have developed a high degree of isolation of their swimbladders against diffusion (low F) as a means for reducing gas loss.

We may now scrutinize somewhat further the idea that the nitrogen deposited into the swimbladder to develop a pressure $\left(\frac{a}{100} D\right)$ is a more or less constant fraction of the oxygen pressure $\left(\frac{100 - a}{100} D\right)$. In Figure 1 we have plotted curves for a series of a values (0, 2, 15, 80 and 100), according to equation (1). It will be seen that curves calculated using the a values of 2 and 15 describe fairly well the upper and lower limits of nitrogen admixture in the deposited swimbladder gas of our marine fishes. A fish like *Coregonus* which deposits near to 100% nitrogen would be expected to present a nitrogen percentage increasing with depth. A fish with an a value of 80 would maintain this percentage at all depths. We have no explanation why there seems to be a gap in the a values between some 20 and 90–100. As indicated by Figure 3 and by Hüfner's data, a seems to be a species characteristic.

Hüfner (1892) found that six out of nine whitefish (*Coregonus acronius*) from 60 to 80 meters' depth in the Bodensee had a nitrogen content in their swimbladders of 99–100%. At the surface these fishes were bloated with enough gas to make them buoyant at the bottom, and they must hence have deposited their nitrogen against a hydrostatic pressure of some 6–8 atmospheres (*cf.*, Scholander *et al.*, 1951). The data have been entered in Figure 1 and agree with the ideas embodied in equation (1). It is a pleasure to record that these seemingly incredible findings have lately been fully corroborated and extended by observations on fishes from the Great Lakes made by Mr. R. L. Saunders from the laboratory of Dr. F. E. J. Fry, Department of Zoology, University of Toronto.

Composition of the Gas Secreted

We have so far discussed the gas composition as it is found in the swimbladder at various depths, which leads us to believe that deep sea fishes deposit in their swimbladders not pure oxygen, but oxygen together with a fraction, a, of inert gases ("nitrogen"), a being high in some species and low in others. We shall now consider to what extent the a values might reveal what is the composition of the gas that has actually been secreted.

The gas pressure in the swimbladder in excess of the one atmosphere due to the combined pressure of nitrogen + oxygen in the sea water is the resultant of (1) the gas secretion into the bladder and (2) the diffusion losses through its wall. The swimbladder in deep sea fishes is capable of maintaining with low gas loss a pressure gradient of one hundred or more atmospheres through the thin air bladder

wall, and it is therefore clear that the exit mechanism for the gases constitutes a potent diffusion barrier. It seems likely that the secreted gases at sub-maximal depths are produced with a pressure substantially higher than the ambient hydrostatic pressure. Only if the diffusion coefficients for the different gases were the same could the gas composition in the swimbladder equal the composition of the secreted gas. The diffusion coefficient for nitrogen through a variety of animal tissues has been found to be only around one half of that of oxygen (Krogh, 1919). The steady state requires that the molar amount of each gas leaving the bladder through diffusion loss should equal the molar amount secreted. A steady state can therefore occur only when the swimbladder has backed up enough partial pressure for each gas component to allow it to pass the diffusion barrier in an amount equal to that secreted. The pressures of nitrogen and oxygen accumulated in the swimbladder above the ambient partial pressures were empirically found to be $\frac{a}{100} \times D$ atmospheres and $\frac{100 - a}{100} \times D$ atmospheres respectively (equation (1)). The diffusion losses, and therefore secretion, of these gases would hence be $\frac{a}{100} \times D \times n$ and $\frac{100 - a}{100} \times D \times o$, where n and o are the diffusion coefficients for nitrogen and oxygen respectively. Recalculated on a per cent basis, the secreted nitrogen percentage, N_{2_s}, would relate to a according to

$$N_{2_s} = \frac{100\ a}{\frac{o}{n}(100 - a) + a}. \qquad (2)$$

With the ratio of $o/n = 2/1$, the secreted N_2 percentage would be $\frac{100\ a}{200 - a}$. This means that for low values of a, like the ones found, it might be anticipated that the secreted mixture would have a *nitrogen* percentage equal to about $\frac{1}{2}\ a$. Conversely, if a were near 100, as found in *Coregonus,* the *oxygen* percentage of the secreted gas would be about twice as high as the oxygen percentage found. Thus, if the nitrogen percentage in the swimbladder of a fish at 1000 meters' depth is found to be 4.8%, then a is 4.0% and the secreted mixture is likely to be 2% N_2 and 98% O_2. If in a *Coregonus* the a value is 95, the secreted gas is likely to be 90% N_2 and 10% oxygen.

Schloesing and Richard (1896) found the argon fraction in the swimbladder "nitrogen" to be some 60% higher than in air. From the solubility of argon in water and its molecular weight one would expect argon to have twice as high a diffusion coefficient through animal tissue as nitrogen. If, therefore, argon and nitrogen entered the swimbladder in the same ratio as in air one would expect a lower argon fraction in the swimbladder rather than a higher. Evidently, therefore, these two gases enter the swimbladder in proportions different from those in air. We are totally in the dark as to how the presumably inert argon and nitrogen have attained the high pressures found in the swimbladder.

We wish to express our gratitude to Dr. Alfred C. Redfield for his stimulating

interest. We were fortunate to have all possible cooperation from Dr. William C. Schroeder, who conducted the deep sea cruises off the New England coast. He identified our specimens and supplied us with information on the depth ranges of the fishes. The Captain and the crew of the dragger *Cap'n Bill II* did everything to facilitate our work on board.

We are indebted to Dr. C. M. Breder, Jr., at the American Museum of Natural History, for arranging our stay at the Lerner Marine Laboratory. We wish to extend our thanks to Mr. Michael Lerner for his generous cooperation in securing deep sea material at Bimini and to Mr. Marshall Bishop for providing us with the most excellent facilities in the laboratory. We wish to thank Mr. Vladimir Walters, of New York University, for his excellent assistance, and we are much obliged to Mrs. Susan I. Scholander for help in the field and in the preparation of the final manuscript.

Summary

1. The composition of the swimbladder gas has been determined in 26 species (260 specimens) of marine deep-sea fishes taken at known depths between 200 and 950 meters.

2. The partial pressure of nitrogen in the bladder steadily increases with depth until it reaches some 5–15 atmospheres at a depth of 900 meters, revealing that not only oxygen but also nitrogen is transported into the swimbladder against a considerable gradient. This corroborates the findings of Hüfner (1892) that the whitefish (*Coregonus*) is able to secrete pure nitrogen against a hydrostatic pressure of 6–8 atmospheres.

3. The data, together with previous observations from shallower depths, show that the nitrogen tension at all depths may be expressed by (1) a diffusion term of 0.8 atmosphere, plus (2) a secretion term which, although different for different species of fish, is in each species a constant percentage of the total secreted gas pressure. Among our fish the secretion term ranges from about 2% to 15% nitrogen. In the whitefish it is apparently 100%. In a steady-state situation the percentage nitrogen actually secreted into the swimbladder is probably lower than the nitrogen percentage indicated by the secretion term because oxygen is more easily lost by diffusion through animal tissue than is nitrogen.

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